Originals

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Morphology of *Dictyopteris prolifera* (Dictyotales, Phaeophyceae) with Special Reference to Reproductive Organs

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Tetrasporophytes and female and male gametophytes of *Dictyopteris prolifera* (Okamura) Okamura (Dictyotales, Phaeophyceae) were collected in Pacific coast of Japan. This is the first report of the male gametophyte from field collections. Tetrasporangial sori and gametangial sori are produced on both sides of blades. Tetrasporangial sori develop in belts along both sides of the midrib. Male and female gametangial sori are scattered on both sides of the midrib. With the further maturation, tetrasporangial sori and male and female gametangial sori sometimes extend toward the midrib. Tetrasporangia are spherical or elliptical, project above the cortex, and have 1–4 stalk cells at the base. In a tetrasporangial sorus, sporangia in various stages of development are randomly arranged. Oogonia are spherical, obovoid or ellipsoidal, and have a stalk cell at the base. In an oogonial sorus, oogonia at almost the same developmental stage are clustered close together with no space between them. This is the first description within *Dictyopteris* of the tightly aggregated oogonial arrangement. Antheridial sori project above the cortex, and are surrounded by 2–5 rows of immature antheridial cells. An antheridium has 1–2 stalk cells at the base.

Key words: Antheridium, *Dictyopteris prolifera*, Dictyotales, oogonium, tetrasporangium

About twenty species of *Dictyopteris* have been described worldwide (Womersley 1987) and nine of these species grow in Japan (Yoshida 1998). In several species of them, reproductive thalli have been described so far. Tetrasporophytes and female and male gametophytes were reported for the Japanese specimens of *D. divaricata* (Okamura) Okamura (Tanaka 1992) and *D. undulata* Holmes (Tanaka 1998), and the Australian specimens of *D. acrostichoides* (J.Agardh) Børgesen (Phillips 1988), *D. australis* (Sonder) Askenasy and *D. muelleri* (Sonder) Reinbold (Phillips 1998). Tetrasporophytes and male gametophytes of *D. polypodioides* (DC.) Lamouroux (Johnson 1891, Tanaka 1944, Khatoon and Begum 1990 as *D. membranacea*) and female and male gametophytes of *D. fucoides* Tanaka (Tanaka 1960) have been previously described. In some other species, e.g., *D. latiuscula* (Okamura) Okamura (Okamura 1907), *D. plagiogramma* (Montagne) Vickers (Allender and Kraft 1983) and *D. serrata* (Areschoug) Hoyt (Phillips and Huisman 1998), only the tetrasporophyte has been described. These descriptions were, however, often incomplete in anatomical respects.

Dictyopteris prolifera was first described by Okamura in De Toni and Okamura (1894) as *Halyseris prolifera*. This species is endemic to Japan and its vicinity. In the description of the reproductive organs, oogonial sori were illustrated as 'Oosporen-sori', without explanation about their anatomy. Kumagae (1970) described the developmental stages of the tetrasporangia of *D. prolifera*, but no report has been made on the antheridia. We collected mature sporophytes and female and male gametophytes of *D. prolifera* in the Izu and Boso regions of central Pacific Japan. From these collections, we attempt to describe the morphology and anatomy of *D. prolifera*, with special reference to the reproductive organs. The reproductive organs are compared among the species of *Dictyopteris* in their morphological respects.

Materials and Methods

Dictyopteris prolifera was collected from three sites on the Pacific coast of Japan (Table 1). Thallus tissue was fixed in a solution of formalin and seawater (1 : 9) soon after collection, and thus preserved for detailed anatomical examination. Observations of reproductive organs were made from fully matured plants. Sections for microscopic examination were made from liquid preserved specimens on a freezing microtome. They were stained with 1 % aqueous aniline blue solution, and mounted in a 2 : 3 mixture of water and corn sugar syrup, with a little formalin, as semi-permanent slides. Differential interference contrast (DIC) optics (Nomarski apparatus, Nikon) was used for some photographs. Specimens examined have been deposited in the Museum of Tokyo University of Fisheries (MTUF-AL). The size of each part of thallus was measured, and the means and standard deviations were calculated. Photographs are based on MTUF-AL-F 319 and 719 (sporophyte), 728 (female gametophyte) and 519 and 724 (male gametophyte).

Results

Dictyopteris prolifera (Okamura) Okamura, Rec. Oceanogr. Works Japan **2**: 102 (1930) – *Haliseris prolifera* Okamura in De Toni and Okamura, Ber. deut. bot. Ges. **12**: 74, pl. 16, f. 1–5 (1894) – *Halyseris* (= *Haliseris*) *prolifera* Okamura, Nippon Sourui Meii, 110 (1902); Icon. Jap. alg. **1**: 55, pl. 12 (1907) – *Neurocarpus prolifera* (Okamura) Kuntze, Revis. gen. pl. 417

Table 1. Localities and dates of the specimens collected of *Dictyopteris prolifera*

Locality	Date	Phase*	Specimen No. (MTUF-AL-F)
Shikine Isl., Izu Islands, Tokyo Pref.	Apr. 30, 1998	S	318–320, 322–324, 719, 722, 727
		F	721, 728
		M	720, 724
	July 2, 1999	S	679–688
		M	677, 678
Shimoda, Izu Peninsula, Shizuoka Pref.	Oct. 3, 1998 (Cast up)	M	519
Tateyama, Boso Peninsula, Chiba Pref.	May 17,1999 (Cast up)	S	647

*S: sporophyte. F: female gametophyte. M: male gametophyte.

(1898); Okamura, Nippon kaisô shi 174 (1936).

Japanese name: Hera-yahazu.

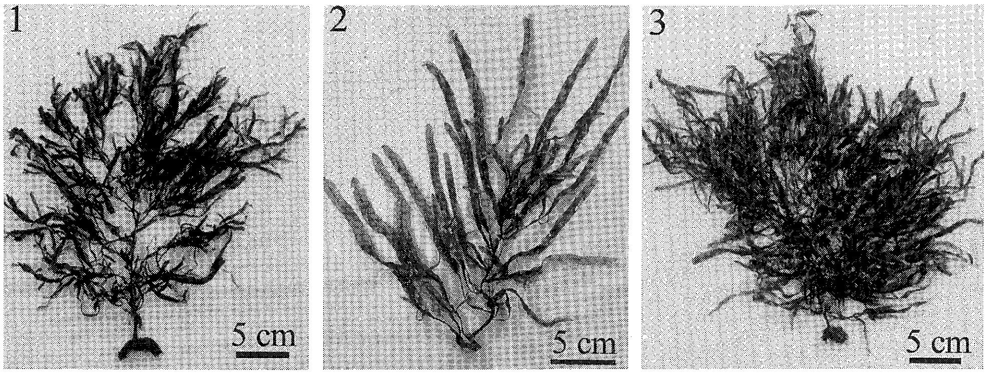
Representative specimens examined: Shikine Isl., Tokyo Pref., Japan (K. Hasegawa, Apr. 30, 1998, MTUF-AL-F 318–320, 322–324, 719, 722, 727, sporophyte; MTUF-AL-F 721, 728, female; MTUF-AL-F 720, 724, male; K. Hasegawa, July 2, 1999, MTUF-AL-F 679–688, sporophyte; MTUF-AL-F 677, 678, male); Shimoda, Shizuoka Pref., Japan (K. Hasegawa, Oct. 3, 1998, MTUF-AL-F 519, male); Tateyama, Chiba Pref., Japan (K. Hasegawa, May 17, 1999, MTUF-AL-F 647, sporophyte).

Dictyopteris prolifera grows attached to rocks in the upper subtidal zone in areas of medium wave action. Mature plants are found from spring to autumn. Fully matured sporophytes, male and female gametophytes (Figs. 1–3) were collected on April 30, 1998 at Shikine Isl. of the Izu Islands. Fully matured male gametophytes were also collected on October 3, 1998 from Shimoda, Izu Peninsula.

Plants consist of an erect thallus of approximately 30 to 70 cm in height, arising from a holdfast. The thallus is dark brown in color and is composed of many blades with a midrib and wing. Dichotomous branching rarely occurs and lateral, secondary or tertiary proliferous branches (Fig. 4) commonly arise from the midrib, so that each branch is not arranged in one plane on the thallus. The primary branch arising from a holdfast reaches about 1cm width. The holdfast, formed from a number of multicellular and filamentous rhizoids, is spongy and tightly attached to the substratum.

The blade consists of a medulla and cortex. The midrib is composed of large medullary cells and a layer of peripheral cells in the outer region (Fig. 5). The blade length attains over 30 cm in secondary branches, which arise from a primary branch. The thickness of a blade decreases from the midrib toward the margin. The midrib includes 12 to 18 layers of medullary cells that are cylindrical and elongated in longitudinal sections (Fig. 7).

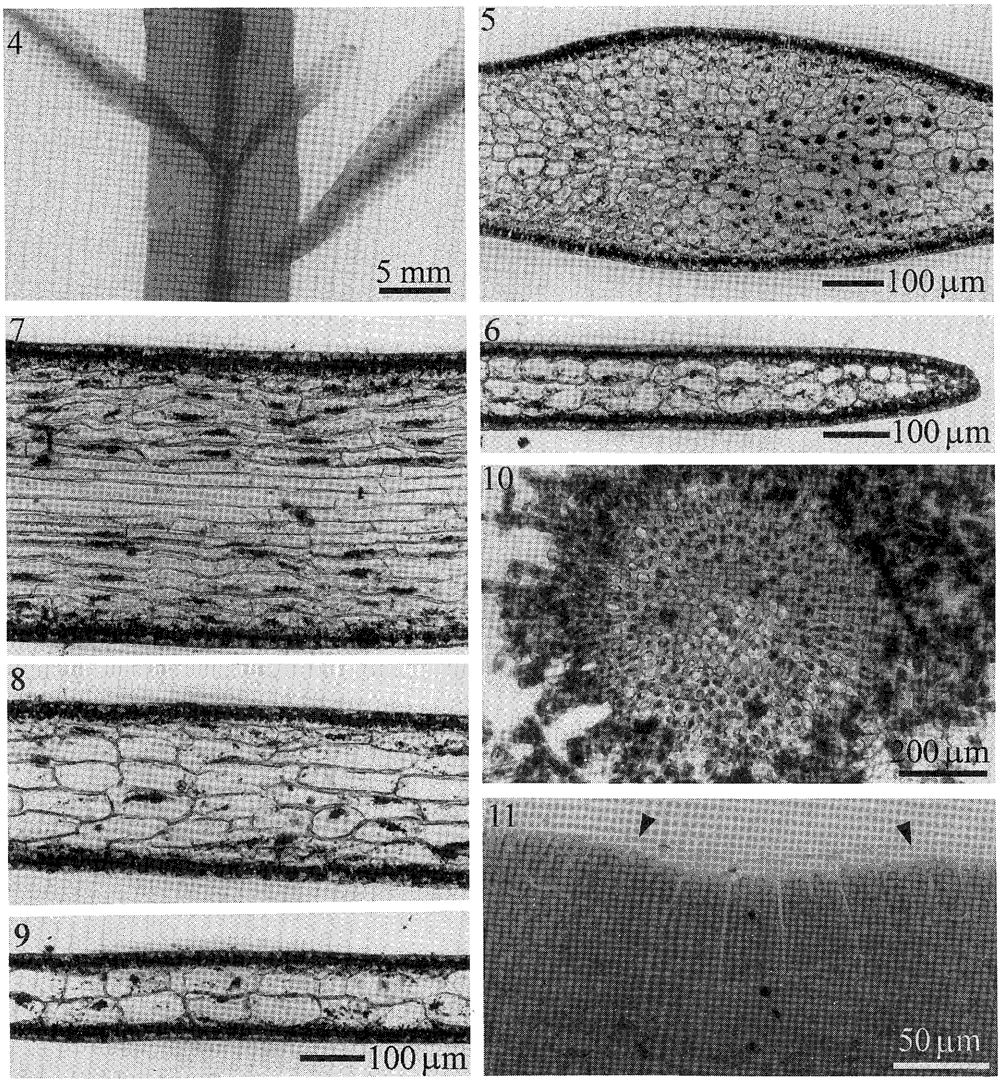
The wing is composed of two to five layers of medullary cells in the middle region between the midrib and margin (Fig. 6). All the cells of a wing are obliquely arranged to the midrib at an angle of about 30 degrees. The medullary cells of the wing are thicker than those of the midrib. The lower region of the thallus (Fig. 10) has no wing and the cell walls of the peripheral medullary cells are thickened. Cortical cells of the lower region of the thallus give rise to filaments, which become rhizoids of the holdfast. The rhizoid



Figs. 1–3. Mature thalli of *Dictyopteris prolifera*. Fig. 1. Sporophyte. Fig. 2. Female gametophyte. Fig. 3. Male gametophyte.

is thick at the base, and becomes thin and bifurcate toward the tip. Hair pits are scattered over the blade surface. Ten to twenty-eight meristematic cells are arranged in a row at the apex of the blade (Fig. 11), each of which is dark in color and narrow and cylindrical in shape.

Sporophytes, female and male gametophytes are all similar in external morphology and cannot be distinguished from each other

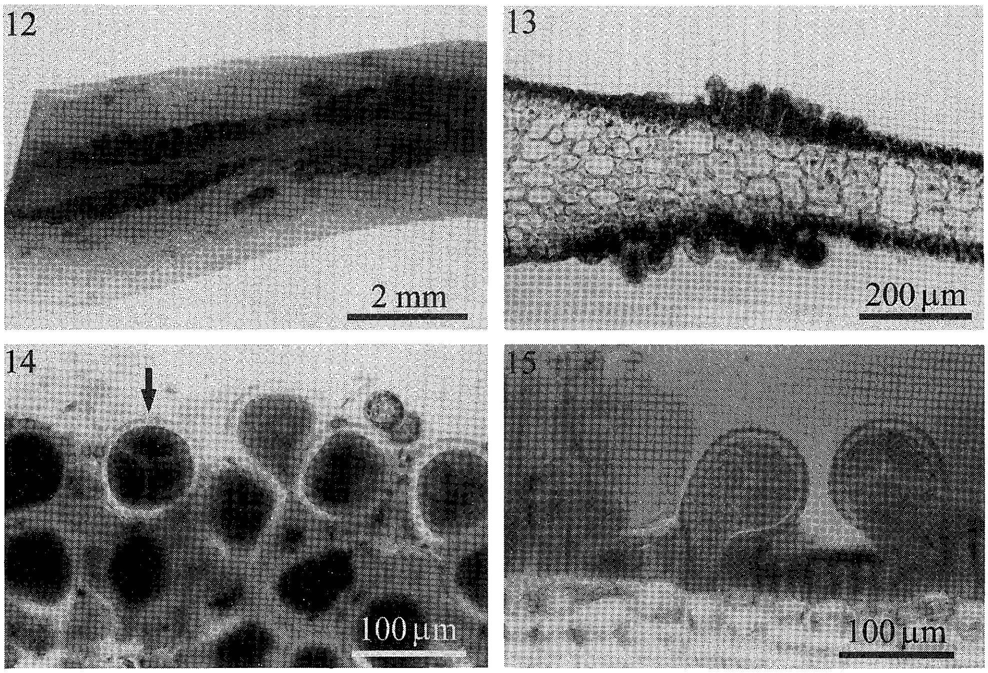


Figs. 4–11. Vegetative structure of *Dictyopteris prolifera*. Fig. 4. Lateral proliferous branches arised from a midrib. Fig. 5. Transverse section of a midrib. Fig. 6. Transverse section of the peripheral region of a wing. Fig. 7. Longitudinal section of a midrib. Fig. 8. Longitudinal section of middle part of a wing. Fig. 9. Longitudinal section of peripheral region of a wing. Fig. 10. Transverse section of lower midrib, which lacks wing. Thick walls of peripheral medullary cells are seen. Cortical cells giving rise to filaments are also seen. Fig. 11. Apical meristem. Meristematic cells, showed between two arrow-heads, are more elongated and narrower than adjacent cells. Scale bar of Fig. 9 applies to Figs. 7–8.

when they are immature. Tetrasporangia, oogonia and antheridia are formed in sori on both surfaces of a blade in the upper and middle regions of the thallus. Tetrasporangia are produced along the midrib. Oogonial and antheridial sori are scattered near the midrib. Oogonial sori are arranged obliquely to the midrib. Each tetrasporangial and gametangial sorus is initially formed on the wing along both sides of the midrib. With the progress of maturation, they expand and spread over the midrib.

Development of tetrasporangia

Tetrasporangial sori are produced in dark brownish lines to the naked eye (Fig. 12), which are initially narrow and short, or small spots. Later, each sorus gradually expands and unites with adjacent sori to make large belt-shaped sori that are irregular and indistinct in outline. Well-developed sporangial sori attain 1.8 mm width and the continuous sori extend from the basal region to near the tip of the blade. Sporangia in various developmental stages (immature, just before tetrahedral division, tetrahedrally divided and empty) are mingled within the sorus (Fig. 14). Adjacent sporangia are close in maturity. The sporangial sori are not coated with an indusium. In well developed tetrasporangia, a colorless and transparent layer can be seen between the sporangial wall and the tetraspore mother cell. Immature sporangia have no transparent layer. The initial cell of a tetrasporangium is produced from a cortical cell, which differentiates into a tetrasporangium and several stalk cells at the

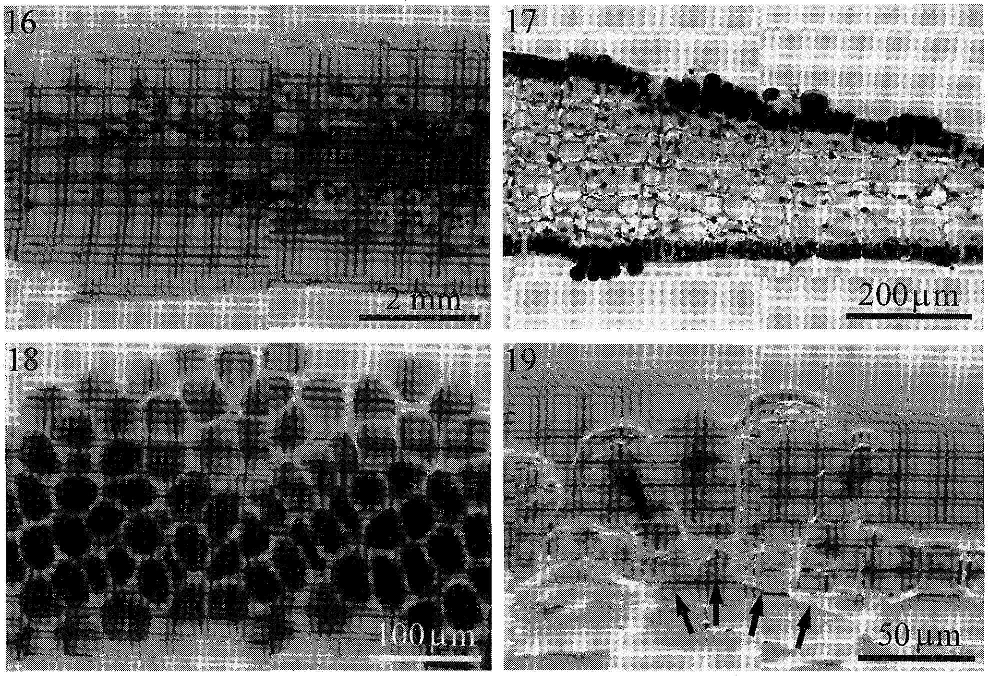


Figs. 12–15. Sporangia of *Dictyopteris prolifera*. Fig. 12. Surface view of a blade, producing belts of tetrasporangial sori on both sides of a midrib. Fig. 13. Transverse section of a blade producing tetrasporangial sori. Various sized sporangia are produced on both sides of the blade. Fig. 14. Surface view of a tetrasporangial sorus. Tetraspores can be seen in a sporangium (arrow). Fig. 15. Transverse view of two tetrasporangia, tetrahedrally divided.

base. Mature tetrasporangia (Fig. 15) project above the cortex, are spherical to elliptical, 68 to 124 µm (97 ± 9 µm) in diameter and 78 to 149 µm (123 ± 15 µm) in height and born on one to four stalk cells. Stalk cells are 12 to 47 µm (26 ± 5 µm) in diameter and 6 to 31 µm (14 ± 5 µm) in height. The piled stalk cells are often wider close to the sporangium, tapering to the base of the stalk. However, the heights of those cells are irregular to their position to the sporangium. After liberation of spores, the sporangial wall is broken at the top and remains attached to the upper part of the stalk cell. Liberated spherical spores are 55 to 65 µm in diameter.

Development of oogonia

Oogonial sori are lighter brown in color and clearer in outline than tetrasporangial sori (Fig. 16). Their outlines are initially elliptical and later become irregular by expansion of each sorus and by uniting with adjacent sori. In every sorus, oogonia are aggregated, and they are at almost the same stage of development. Oogonia are tightly packed with no space between them (Fig. 18), and not coated with an indusium. Oogonial sori contain several to more than a hundred oogonia, reaching a maximum size of approximately 2.5 mm in width and 5 mm in length. Oogonia do not have a transparent layer within and thus resembles immature sporangia. The initial cell of an oogonium is derived from a cortical cell, and it produces an oogonium and a stalk cell. Mature oogonia (Fig. 19) project their upper part above the cortex, and are spherical, obovoid

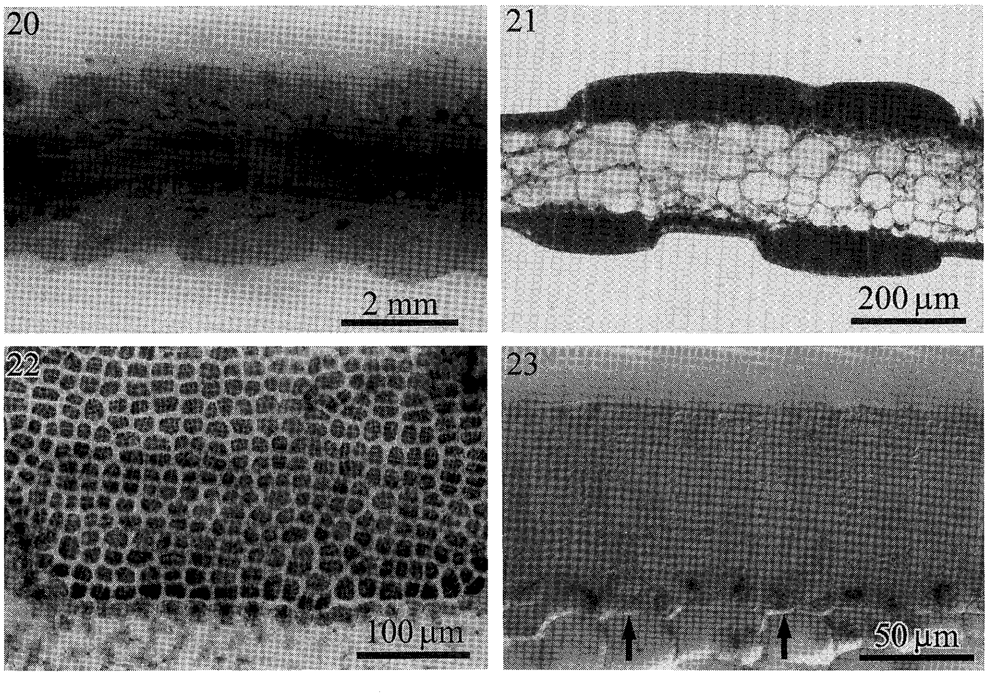


Figs. 16–19. Oogonia of *Dictyopteris prolifera*. Fig. 16. Surface view of a blade with oogonial sori. Oogonial sori are scattered on both sides of a midrib. Fig. 17. Transverse section of a blade with oogonial sori on the both surfaces. Fig. 18. Surface view of an oogonial sorus. Oogonia are almost the same in size and tightly aggregated. Fig. 19. Transverse view of oogonia. Each of oogonia has a stalk cell at the base (arrows).

or ellipsoidal, 22 to 46 μm (35 ± 6 μm) in diameter and 27 to 75 μm (57 ± 11 μm) in height. The size of stalk cells are 14 to 27 μm (20 ± 3 μm) in diameter and 14 to 35 μm (23 ± 6 μm) in height. After liberation of an egg, the oogonial wall remains attached to the upper part of the stalk cell.

Development of antheridia

Antheridial sori are easily distinguished from tetrasporangial and oogonial sori with the naked eye by their whitish color. Their outlines are elliptical early in development, but become irregular as maturation progresses (Fig. 20). A well-developed antheridial sorus is 3.5 mm wide and 3 cm long in surface view, and projects above the cortex. Antheridia are densely packed within a sorus without any space. Each antheridial sorus is completely surrounded by a vegetative layer (Fig. 22), which is composed of rows of two to five immature antheridial mother cells. The antheridial mother cell is produced by the elongation of a cortical cell, and later differentiates into an antheridium with single, or rarely two, piled stalk cells. Antheridial sori expand by the formation of new antheridia in the marginal part. The height of an antheridial mother cell is almost the same as the height of the adjacent antheridium with its stalk cell. The antheridial mother cells of the marginal part of a sorus are often inverted wedge–shaped cells and gradually decrease in height away from the antheridia. mature antheridia (Fig. 23) are 14 to 24 μm



Figs. 20–23. Antheridia of *Dictyopteris prolifera*. Fig. 20. Surface view of a blade with antheridial sori. Well-developed antheridial sori are broad and irregularly outlined. Fig. 21. Transverse section of a blade with antheridial sori on the both surfaces. Antheridial sori project above the cortex. Fig. 22. Surface view of the marginal part of an antheridial sorus. Fig. 23. Transverse view of antheridia. In an antheridium, several longitudinal rows of loculi can be seen. Most antheridia have a stalk cell at the base (arrows).

(18 ± 3 μm) in diameter and 53 to 78 μm (67 ± 6 μm) in height. In transverse sections, 16 to 24 tiers that consist of 4 to 8 squarish loculi are seen in an antheridium. A stalk cell is 13 to 25 μm (17 ± 3 μm) in diameter and 10 to 20 μm (16 ± 3 μm) in height. Each sorus is covered with a thin colorless cuticle until the liberation of antherozoids. After liberation of antherozoids, the antheridial wall disappears and the stalk cells and peripheral immature antheridial mother cells are left.

Discussion

Vegetative structure

On a blade, cells composing the midrib are directed parallel to the growing axis, while cells of the wing are obliquely arranged to that. The medullary cells of the midrib are cylindrical and thinner than those of the wing. Considering the differences in cell shape and arrangement, it is suggested that some differentiation occurs in the midrib and wing. The transverse view of a blade has been adopted as a standard for morphological character among the species of *Dictyopteris* (Khatoon and Begum 1990, Tanaka 1992, 1998, Phillips 1998). For anatomy of *Dictyopteris*, the transverse view cannot show the real dimensions of obliquely arranged cells in the wing, but following this manner is still suitable for avoiding confusion and allowing interspecific comparisons. *Dictyopteris prolifera* branches mainly by lateral proliferation. As for other species of *Dictyopteris*, only *D. latiuscula* shows similarity to *D. prolifera* in branching and thallus structure (pers. obs). The habitat of these two species is restricted to around Japan. Based on the similarity of their thallus morphology and distribution, it is suggested that these two species are closely related.

All of the reproductive organs of *D. prolifera* are produced on both surfaces of a blade. This feature is usual in other species of *Dictyopteris*: *D. divaricata* (Tanaka 1992), *D. undulata* (Tanaka 1998), *D. australis* and *D. muelleri* (Phillips 1998). Tanaka (1960) reported that oogonial sori of *D. fucoides* are usually produced on one side of a blade. However, no further report has been made on *D. fucoides* ever since. In order to discuss the generic characterization of *Dictyopteris*, additional studies of reproductive structure of other species of the genus should be made.

Sporangium

Kumagae (1970) described that the number of sporangial stalk cells of *D. prolifera* is usually two, sometimes three. He stated that two stalk cells are formed preceding the formation of tetraspores. In the present study, we found one to four stalk cells associate with sporangia, which formed tetraspores, contrasting with Kumagae's (1970) findings. Kumagae (1968) also reported that the diameters of liberated spores were 75 to 77 μm in the specimens from Fukuoka, Kyushu, Japan. This value also differs from that of the present study. Phillips (1998) noted that the mean size of sporangia of *D. muelleri* exhibit considerable variation among populations. The same phenomenon may be observed in *D. prolifera.*

Phillips (1998) suggested the occurrence of four different patterns in sporangial distribution. According to her classification, *D. prolifera* is similar to *D. plagiogramma* and *D. polypodioides*, whose pattern of sporangia is 'scattered in longitudinal bands parallel to the midrib'.

Oogonium

Generally, it is difficult to distinguish immature sporangia from oogonia in *D. prolifera* in surface view without closer observations. Sporangial sori are formed along both sides of the midrib, and sporangia in various maturation stages are mingled in a sorus. On the other hand, oogonial sori are scattered over the blade, and almost unisize oogonia are aggregated leaving no space between them. In the description of *D. prolifera* (De Toni and Okamura 1894), only oogonial sori are illustrated as 'Oosporensori', but it is doubtful whether they really show oogonial sori. From the result obtained in the present study, it seems that those figures are probably a mixture of sporangia and oogonia.

Fully matured oogonial sori of *D. prolifera* are not regular in outline, and oogonia are arranged closely within a sorus. This is a characteristic feature of this species. Tanaka (1998) suggested that among the species of *Dictyopteris* the pattern of oogonial aggregation differed from one another. *Dictyopteris acrostichoides* (Phillips 1988), *D. australis* and *D. muelleri* (Phillips 1998) rarely form large oogonial sori, and oogonia are scattered on an extensive fertile zone. *Dictyopteris fucoides* (Tanaka 1960), *D. divaricata* (Tanaka 1992) and *D. undulata* (Tanaka 1998) have elliptical shaped oogonial sori with loosely arranged oogonia. The distribution of oogonia of *Dictyopteris* may be categorized into three types; 'scattered type' (Fig. 24a, *D. acrostichoides* and *D. muelleri*), 'loosely aggregated type' (Fig. 24b, *D. fucoides*, *D. divaricata* and *D. undulata*) and 'tightly aggregated type' (Fig. 24c, *D. prolifera* in the present study).

Antheridium

The blades of male gametophytes with antheridial sori from Shikine Isl. are wider and longer than those grown in Shimoda. Though the sizes of antheridial sori depend on the blade size, the size of each antheridium is not affected by these differences in blade width. Antheridial sori of *D. prolifera* and *D. undulata* (Tanaka 1998) show a similarity in producing large, indistinctly outlined sori through the development and union of young elliptical sori. *Dictyopteris divaricata* (Tanaka 1992) and *D. polypodioides* (Johnson 1891) produce antheridial sori with elliptical outlines, and do not produce large, indistinctly outlined sori.

In *Dictyopteris*, the arrangement of antheridia within a sorus seems similar between species. No space can be seen within a sorus, and the marginal area of antheridial sori are surrounded by antheridial mother cells.

Antheridia of *D. fucoides* (Tanaka 1960) are described as 'nearly cubic' in shape. Antheridia develop from a cortical cells and increase only in height during development. Therefore, the cubic antheridia must be in the middle of developing. Care should be

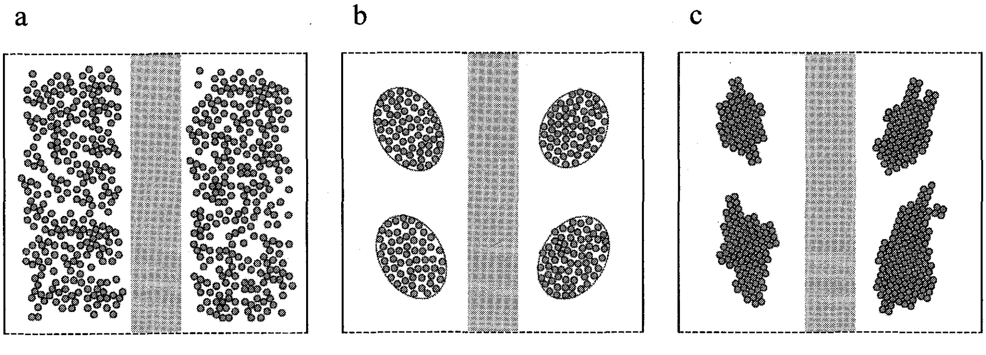


Fig. 24. Three types of oogonial distribution in *Dictyopteris*. a: scattered type. (*D. acrostichoides*, *D. australis* and *D. muelleri*) b: loosely aggregated type. (*D. divaricata*, *D. fucoides* and *D. undulata*) c: tightly aggregated type. (*D. prolifera* in the present study)

taken to measure and report the size of reproductive organs at various stages of development to provide a detailed description of each species.

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長谷川和清，田中次郎：ヘラヤハズ（褐藻，アミジグサ目）の形態，特に生殖器官について

ヘラヤハズの四分胞子体及び雌雄の配偶体を太平洋沿岸から採集した．雄性配偶体の採集は今回が最初の報告である．四分胞子嚢及び雌雄の配偶子嚢は葉片の両面に形成される．四分胞子嚢群は中肋の両側に沿って帯状に発達し，雌雄の配偶子嚢群は中肋の両側に散在し，いずれも成熟に伴って広がり中肋上に及ぶことがある．四分胞子嚢は球形から楕円体で皮層の上に突出し，基部に1–4個の柄細胞を持つ．胞子嚢群には，様々な発達段階の胞子嚢が混在する．生卵器は球形，倒卵形あるいは楕円体で，基部に1個の柄細胞を持つ．生卵器群にはほぼ均一な発達段階の生卵器が密集する．造精器群は周囲を2–5列の造精器母細胞で囲まれ，皮層上に盛り上がるようにして形成される．造精器は角柱状で，基部に1–2個の柄細胞を持つ．生卵器が密集して形成される状態は，これまでに報告されているヤハズグサ属の他の種には見られない特徴である．　（東京水産大学資源育成学科）